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Variable Population Structure and Tenacity in the Intertidal Chiton *Katharina tunicata* (Mollusca: Polyplacophora) in Northern California

by

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Abstract. Populations of the chiton *Katharina tunicata* (Wood, 1815) were studied at three rocky intertidal areas in northern California, each subjected to a different degree of wave exposure. The spatial density and size structure of *Katharina* populations varied with the degree of exposure to wave action. Chiton densities increased and body sizes decreased with increased exposure to wave action. Laboratory experiments showed that tenacity (adhesion strength, or resistance to shear force) of *Katharina* significantly increased with a decrease in body size. This increased capacity of smaller chitons to resist removal from the substratum may provide a mechanism for the observed patterns of abundance and size-distribution of *Katharina*.

INTRODUCTION

Organisms living in rocky intertidal areas on exposed shores encounter a number of biological and environmental factors that interact to regulate population and community structure (see reviews by CONNELL, 1972; STEPHENSON & STEPHENSON, 1972; RICKETTS *et al.*, 1985). Waves are an important agent of disturbance on rocky shores and may be extremely important in structuring intertidal populations and communities (*e.g.*, JONES & DEMETROPOULOS, 1968; PAINE & LEVIN, 1981; DENNY, 1985; DENNY *et al.*, 1985). Analyses of intraspecific variation of important intertidal organisms at sites varying in exposure may yield information critical to our understanding of community ecology.

Chitons are conspicuous components of intertidal communities in many areas of the world (BOYLE, 1970; GLYNN, 1970; PAINE, 1980; DETHIER & DUGGINS, 1984; DUGGINS & DETHIER, 1985; OTÁIZA & SANTELICES, 1985). The role of motile herbivores like chitons in regulating algal composition and ultimately community structure may be extremely important (PAINE & VADAS, 1969; DAYTON, 1975; LUBCHENCO & MENGE, 1978; LUBCHENCO & GAINES, 1981). Aside from studies on reproductive biology (HIMMELMAN, 1978, 1979, 1980; PEARSE, 1978; SAKKER, 1986) relatively little is known about the ecology of intertidal chitons (see BOYLE, 1970; GLYNN, 1970; ANDRUS & LEGARD, 1975; DETHIER & DUGGINS, 1984; DUGGINS & DETHIER, 1985; OTÁIZA & SANTELICES, 1985).

The chiton *Katharina tunicata* (Wood, 1815) (hereafter as *Katharina*) is an important member of mid- to low-intertidal communities along the Pacific coast of North America (HIMMELMAN, 1978; DETHIER & DUGGINS, 1984; DUGGINS & DETHIER, 1985), and has a geographic range from Alaska to southern California (HADERLIE & ABBOTT, 1980; RICKETTS *et al.*, 1985). Despite the abundance and importance of *Katharina* in structuring intertidal communities (DETHIER & DUGGINS, 1984; DUGGINS & DETHIER, 1985) little is known regarding intraspecific variation in this chiton.

Preliminary observations suggested that the population structure of *Katharina* varied at different sites in northern California. In this study abundances and size distributions of *Katharina* were quantified at three rocky intertidal areas and correlated with the degree of wave exposure at the sites. In addition, the tenacity (adhesion strength) of chitons was measured in the laboratory to determine if tenacity varied with body size. Finally, several alternative hypotheses are discussed that may explain the observed patterns of *Katharina* population structure.

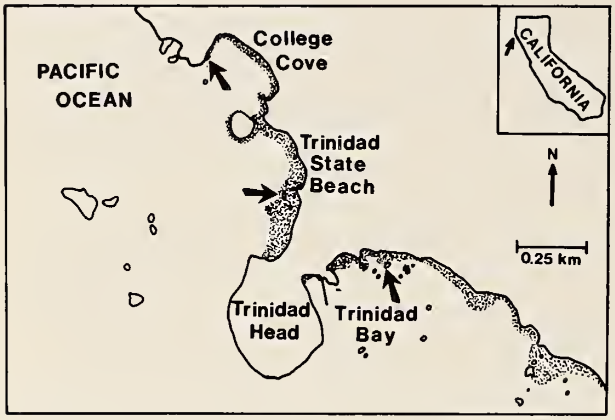

Figure 1

Location of study areas (arrows) near Trinidad, northern California (41°03′07″N, 124°07′51″W). In order of decreasing exposure to wave action the study sites are Trinidad State Beach, College Cove, and Trinidad Bay.

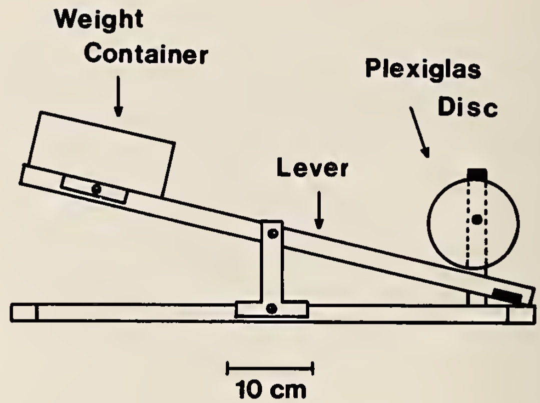

Figure 2

Apparatus used to measure tenacity of chitons on a hard substrate (Plexiglas) and subjected to shear forces.

MATERIALS AND METHODS

Study Areas

The study was conducted at three rocky intertidal areas near Trinidad, in northern California (Figure 1). The sites were similar in terms of inclination and heterogeneity of the substratum and were covered primarily with crustose coralline algae and clumps of the laminarian *Hedophyllum sessile* (C. Agardh) Setchell. *Katharina tunicata* was the most prominent herbivore at the sites, although the limpets *Lottia pelta* (Rathke, 1833) (=*Collisella pelta*) and *Tectura scutum* (Rathke, 1833) (=*Notoacmea scutum*) were also common. The seastar *Pisaster ochraceus* (Brandt, 1835) occurred at all sites below the zone of *Katharina*, although it was more abundant at the most exposed site.

Transects were initially established at each study site through belts of *Hedophyllum* at about 0.5 m below to 0.5 m above mean lower low water. These transects were oriented perpendicular to the direction of wave impact and marked by permanent 5-cm^2 markers bolted to the substratum.

The three study areas differ in their degree of exposure to wave action. Trinidad State Beach faces west-northwest and receives the full force of waves and swells. College Cove is slightly protected from wave action by a projecting headland. The south-facing Trinidad Bay site is largely protected from most waves and swells by Trinidad Head and numerous offshore rocks. A more objective "exposure index" similar to that described by Menge (1976) was calculated for each area (Table 1) and supported the subjective observations. In order of decreasing exposure to wave action, the study areas were Trinidad State Beach, College Cove, and Trinidad Bay.

Table 1

Exposure indices at three study areas in northern California from April 1980 to April 1981. Exposure index = (no. of transect markers lost ÷ no. of marker-months) × 100. A marker-month is one marker in place for 1 month.

Study area	Exposure index
Trinidad State Beach	26.9 (7/26)
College Cove	13.8 (4/29)
Trinidad Bay	0 (0/36)

Sampling Procedures

Katharina populations were examined monthly at each site over a 13-month period from April 1980 to April 1981, except in January 1981 when severe wave action prohibited access. Monthly population densities and size-class distributions were estimated from 10 randomly chosen 0.25-m^2 quadrats along the transects at each study site. All chitons occurring within the quadrats were counted, and body lengths measured to the nearest 0.1 mm with calipers. Mean numbers of individuals per 0.25 m^2 and mean body lengths were calculated monthly for each site.

Experimental Procedures

Sixty-four individuals of *Katharina* between 1.0 and 10.0 cm in body length were studied to determine if their ability to resist removal from a hard substrate (defined as tenacity) varied with body size. Chitons were collected near the field sites between April and August 1981 and maintained in running seawater aquaria at the Telonicher Marine Laboratory (Trinidad, California) of Humboldt State University. All test specimens were used within 2 weeks of collection and each animal was used in only one test. Only healthy animals were tested. Tenacity, expressed as the force per unit area required to dislodge a chiton, was measured using an apparatus that applied a shear force parallel to the chiton's foot (Figure 2). Test substrates

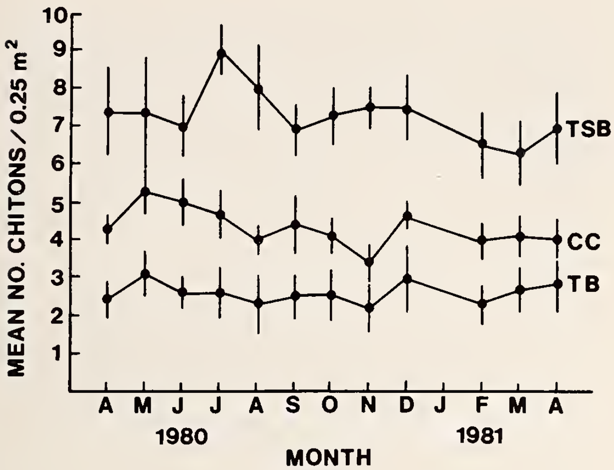

Figure 3

Population densities of *Katharina tunicata* at Trinidad State Beach (TSB), College Cove (CC), and Trinidad Bay (TB) in northern California. Data for each month are expressed as mean number of chitons per 0.25 m^2 ± 1 SE.

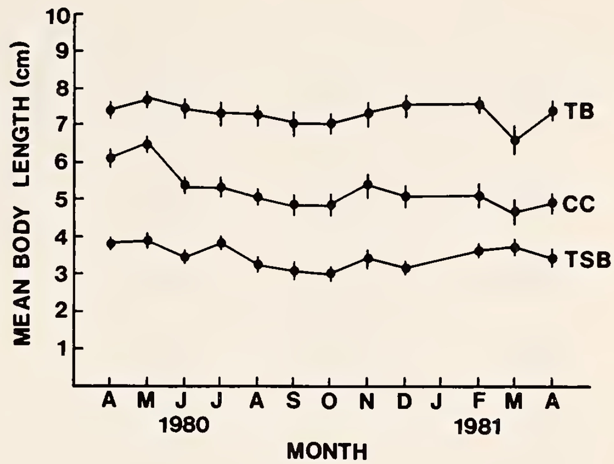

Figure 4

Mean body sizes of *Katharina tunicata* at Trinidad State Beach (TSB), College Cove (CC), and Trinidad Bay (TB) in northern California. Data for each month are expressed as mean body length (cm) of chitons ± 1 SE.

were roughened Plexiglas discs 10 cm in diameter. Chitons were allowed to remain attached to the test surface for approximately 2 h prior to testing. After attachment, the test disc was attached to the apparatus and the lever positioned parallel to the plane of the foot of the attached chiton. Each individual was tapped lightly immediately before testing to induce it to adhere to the substratum as tightly as possible. Weights were then added to the container in 25 g increments every 2.5 sec until the chiton was dislodged from the surface; the maximum weight (g) necessary to cause detachment was recorded. The body length and weight of each individual were measured after testing. The foot surface area (cm^2) was determined by placing the chiton on a transparent grid. Tenacity was calculated as total weight applied per foot area, and converted to newtons per m^2 ($N \cdot m^{-2}$).

RESULTS

Abundance and Size Distribution

The average numbers of *Katharina* per 0.25 m^2 were plotted over the study period for each study site (Figure 3). These mean densities throughout the year differed significantly between sites ($P < 0.005$; Kruskal-Wallis Analysis of Variance). The chiton densities at Trinidad Bay were significantly lower than at College Cove and Trinidad State Beach, and the densities at College Cove were significantly lower than those at Trinidad State Beach ($P <$ 0.001; Mann-Whitney U-test). The densities during the study ranged from 0 to 16 chitons per 0.25 m^2. The animals tended to aggregate around and under clumps of *Hedophyllum,* accounting for an observed patchiness. Generally there were no significant seasonal trends in density fluctuations. However, the decreases in *Katharina* densities between December 1980 and February 1981 may be related to severe storm activity during that period.

The mean body lengths of *Katharina* were plotted for each area over the study period (Figure 4) and were found to differ significantly between sites ($P < 0.001$; one-way ANOVA). Trinidad Bay chitons were significantly larger than those at College Cove and Trinidad State Beach, and the chitons at College Cove were significantly larger than those at Trinidad State Beach ($P < 0.05$; Student-Newman-Keuls test). The body lengths of individuals ranged from 0.72 to 10.15 cm during the study with maximum mean lengths occurring in May 1980 at all sites. The size-class distributions clearly show the distinct nature of the three *Katharina* populations (Figure 5). Greater than 70% of the chitons at Trinidad State Beach, the most exposed site, were consistently less than 5.0 cm in length, while chitons in this size range consistently made up less than 20% of the population at the least exposed site, Trinidad Bay. The size range of College Cove chitons was intermediate between the two extreme sites.

Recruitment

Katharina grows to a length of 2.5 cm during its first year (Hyman, 1967). The relative frequency of juvenile chitons less than 2.0 cm long was plotted for each site over the study period and used as an estimate of recruitment (Figure 6). From these data it appears that recruitment differed significantly at the sites, at least immediately preceding and during this study. Juveniles of *Katharina* were a conspicuous component of the chiton population throughout the year at Trinidad State Beach, with a noticeable peak following the summer of 1980. This peak corresponds with a main spawning period in June as reported by Him-

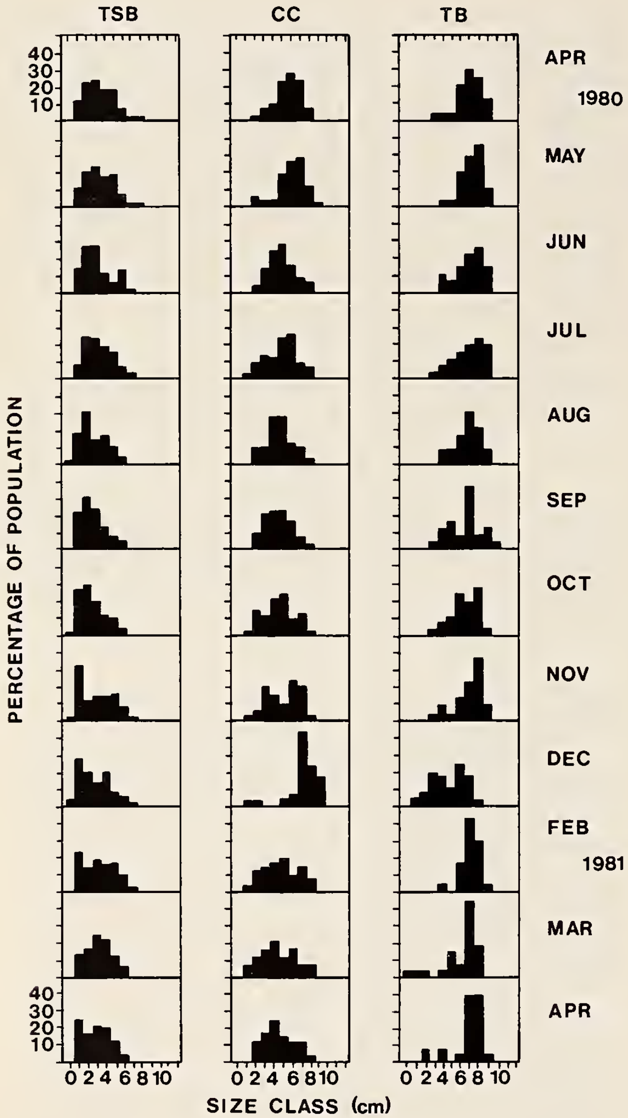

Figure 5

Katharina tunicata. Size-frequency distributions of chitons at three study areas in northern California: Trinidad State Beach (TSB), College Cove (CC), and Trinidad Bay (TB).

MELMAN (1978). In contrast, juveniles were much rarer at the other two study sites.

Juvenile *Katharina* occurred in five different microhabitats during low tides: (1) in cracks or crevices on exposed surfaces, (2) in cracks or crevices under blades of *Hedophyllum,* (3) on bare rock or coralline crusts under *Hedophyllum* blades, (4) under adult *Katharina*, and (5) within *Hedophyllum* holdfasts. Another chiton, *Lepidochitona dentiens* (Gould, 1846) (=*Cyanoplax dentiens*), often coexisted with *Katharina* juveniles within kelp holdfasts.

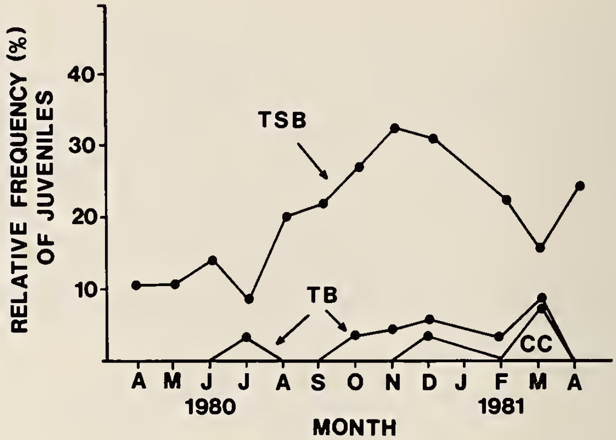

Figure 6

Recruitment of *Katharina tunicata* as estimated by the relative frequency of juveniles (length < 2.0 cm) in chiton populations at Trinidad State Beach (TSB), College Cove (CC), and Trinidad Bay (TB).

Tenacity

There was a significant decrease of tenacity ($N \cdot m^{-2}$) with increasing body size ($P < 0.001$; see Figure 7). Small chitons (2–3 cm long) were up to twice as resistant to removal as were large individuals (8–10 cm). Resistance of animals ranged from 0.87×10^4 $N \cdot m^{-2}$ (a 9.31 cm individual) to 5.10×10^4 $N \cdot m^{-2}$ (a 2.16 cm individual and a 2.49 cm individual). Mean tenacity for all *Katharina* tested ($n = 64$) was $2.45 \pm 1.00 \times 10^4$ $N \cdot m^{-2}$ ($\bar{x} \pm$ SD). LINSENMEYER (1975) reported a lower mean resistance value for *Katharina* equivalent to $1.45 \pm 0.38 \times 10^4$ $N \cdot m^{-2}$ ($n = 12$); however, he provided no data on body sizes. Linsenmeyer's lower value may simply reflect his use of larger individuals.

DISCUSSION

Katharina tunicata is a major determinant of intertidal community structure in the eastern North Pacific whose importance stems from its size, density, and generalist feeding behavior (DETHIER & DUGGINS, 1984; DUGGINS & DETHIER, 1985). However, little is known regarding variation between populations of this chiton. *Katharina* was the dominant herbivore at my study sites, averaging approximately 10–36 individuals per m^2. These densities are comparable to those described for more northern populations (PAINE, 1980; DETHIER & DUGGINS, 1984; DUGGINS & DETHIER, 1985). The density and size structure of *Katharina* populations were shown to vary with the degree of exposure to wave action (Figures 3–5). There was an inverse correlation between population densities and body size of chitons at the three study sites; density increased and body size decreased with increased exposure to wave action.

ANDRUS & LEGARD (1975) reported similar observations for *Katharina* in central California. Similar patterns of abundance and size distribution have been reported for other motile invertebrates including limpets in Great Britain (JONES, 1948; SOUTHWARD, 1953; SOUTHWARD & ORTON, 1954; BALLANTINE, 1961) and Australia (MEYER & O'GOWER, 1963). HARGER (1970, 1972) and PAINE (1976a, b) have shown that temperate mussels and seastars also increase in size where wave action is less, while CONNELL (1972) has shown a similar trend for some marine algae. In contrast, OTÁIZA & SANTELICES (1985) reported that the large Chilean chitons *Acanthopleura echinata* (Barnes, 1824) and *Chiton latus* Sowerby, 1825, displayed an opposite trend, with larger individuals occurring in the most exposed habitats.

Patterns of intertidal population and community structure are the result of complex interactions of predation, competition, biological disturbance, exposure to wave action, and the inclination and heterogeneity of the substratum (DAYTON, 1971; MENGE, 1976). The inclination and heterogeneity of the substratum were similar at my three northern California study sites and were probably not responsible for differences between *Katharina* populations. Intraspecific competition was probably not important since neither food nor space ever appeared to be limiting. Interspecific competition was probably minor since no major competitors for the large macrophytic algae (*e.g., Hedophyllum*) occurred in these areas. The only other common herbivores at these sites were the limpets *Lottia pelta* and *Tectura scutum*. These limpets have been described as "indirect commensals" of *Katharina* (DETHIER & DUGGINS, 1984) and probably have little effect on chiton population structure. Predation pressure may vary between sites since the predatory seastar *Pisaster ochraceus* was more abundant at the most exposed site, Trinidad State Beach. Although *Pisaster* is known to eat *Katharina* (PAINE, 1966; DAYTON, 1975; CAREFOOT, 1977), I never noticed an instance of predation in three years of observation. Thus, it seems unlikely that seastar predation plays a major role in regulating chiton populations near Trinidad, although these observations were restricted to periods of low tides. More information on the feeding habits of *Pisaster* during high tides is needed before definitive conclusions can be made regarding the effect of predation on *Katharina*.

Many motile invertebrates (*e.g.,* seastars, limpets, and chitons) can withstand the direct force of waves by adhering tenaciously to the substratum. The effects of wave action on populations of these organisms cannot be easily predicted. However, degree of wave action may have important consequences on the age or size structure of intertidal populations, since waves are more likely to remove large than small individuals from the substratum (DENNY *et al.,* 1985). Larger chitons may have a greater likelihood of being detached because, as body length increases, the area of attachment (*i.e.,* the foot) does not increase proportionately. Consequently, large animals have a greater ratio of body size to attachment surface and higher profile than small individuals, and could be more susceptible to detachment by wave action. If such is the case, wave action could regulate *Katharina* population structure by removing larger animals in greater numbers than small animals. If this hypothesis is correct, one would expect large chitons to be less abundant than small individuals at areas of high wave impact, and more abundant at more protected areas. Such was the case at the northern California sites. These observations suggest that small chitons have an advantage over large individuals at withstanding forces associated with wave shock. Although LINSENMEYER (1975) demonstrated that the force required to dislodge different species of chitons was directly related to the degree of wave action in the habitat of each species, no attempt was made to determine if resistance to removal (tenacity) varied with body size.

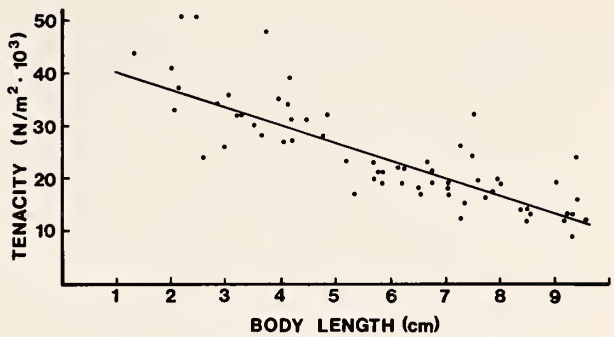

Figure 7

Tenacity of *Katharina tunicata*. Resistance of chitons on a hard substrate (Plexiglas) to removal by a shear force. Least-squares linear regression of tenacity ($N \cdot m^{-2}$) as a function of body size (length in cm). Regression line ($y = 45418 - 3576x$) significant at $P < 0.001$ ($n = 64$).

In this study, there was a significant relationship between the body size and tenacity of *Katharina*; tenacity increased with decreased body size (Figure 7). This increased capacity of smaller chitions to resist removal from the substrate may explain the observed patterns of abundance and size distribution of these animals near Trinidad, by way of limiting the size of chitons at more exposed areas. Although this differential size resistance may explain the observed population structure of *Katharina,* this hypothesis depends upon several assumptions. First, the adhesive abilities of *Katharina* will limit populations only if chitons actually are washed off the substrate. At present there is no direct evidence that they are. Secondly, the chitons must experience shear forces near their adhesive strengths if they are going to be dislodged. This is difficult to determine for *Katharina* because tenacity values were calculated using an unnaturally smooth substrate (Plexiglas), and therefore probably represent underestimates of this chiton's true adhesive abilities (see MILLER, 1974; LINSENMEYER, 1975; DENNY *et al.,* 1985). Furthermore, chitons may not adhere in the lab with a tenacity approaching that in nature. However, these estimates of *Katharina* tenacity ($\sim$1–5 $\times$ 10^4 $N \cdot m^{-2}$) are only an order of magnitude lower than values for limpets ($\sim$1–4 $\times$ 10^5 $N \cdot m^{-2}$) (BRANCH & MARSH, 1978; GRENON & WALKER, 1982; DENNY *et al.,* 1985) on natural surfaces. It seems likely that *Katharina* has adhesive strength at least comparable to limpets under natural conditions. DENNY *et al.* (1985) and others have concluded that, at least for limpets, adhesion is much stronger than typical wave shear. In addition, GLYNN (1970) reported that the Caribbean chitons *Acanthopleura granulata* (Gmelin, 1791) and *Chiton tuberculatus* Linnaeus, 1758, were capable of surviving forces equivalent to those generated by waves 5.5 m high. Finally, there is evidence that normal (lift) forces may be more important than the shear forces measured here (DENNY *et al.,* 1985).

Although the size-resistance hypothesis may explain the observed patterns of abundance and size distribution of *Katharina,* several other alternative hypotheses also explain these patterns. (1) Topographic irregularities (*e.g.,* holes and crevices) may provide greater refuge from wave impact to small chitons than large individuals; large chitons would be selectively removed from areas of high wave impact owing to the lack of suitable refuge. The restriction of juvenile *Katharina* to some type of shelter (under kelp or adult chitons, in cracks or crevices) lends support to this hypothesis. (2) Differential recruitment may be important. Increased recruitment rates at areas at high wave exposure could explain the observed patterns. However, these patterns may be variable in time and space and have little to do with the sites themselves. (3) Less feeding time at areas of high wave impact, due to the increased turbulence in these areas, could cause lower growth rates in chitons; these lower growth rates could result in smaller individuals at areas of high wave exposure. (4) The reduced body size of chitons at areas of high wave shock may be due to increased mortality rates (decreased mean longevity) associated with the severity of the environment.

Knowledge of intraspecific variation of important intertidal species is essential to developing a clear understanding of community organization and structure. More data on chiton hydrodynamics and on feeding times, recruitment, growth rates, and longevity for *Katharina* at areas of varied exposure to wave action are needed to interpret adequately the role that various factors play in regulating the population structure of this animal. Wave action may mediate the population structure of this chiton through complex interactions of some or all of the above proposed hypotheses.

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